A NEW SPECIES OF THE GENUS RHIZOBLEPHARIA FROM THE NEOTROPICS, AND A REDISPOSITION OF THE GENUS IN THE PYRONEMATACEAE, PSEUDOMBROPHILEAE

ROBERT W. ERB[1]

Plant Pathology Herbarium
Cornell University, Ithaca, New York

Rhizoblepharia, erected as a monotypic genus by Rifai *(1968),* was known only from a single Australian collection deposited in the Herbarium of the Royal Botanic Gardens, Kew, England. Rifai's awareness that the delicate transverse wrinkling of the ascospore wall (FIG. 1) was "unique among the Pezizineae" led him to erect a new genus and species on the single collection. That species, *R. jugispora* Rifai, was classified among the Ciliarieae, a tribe established by Boudier *(1907)* to include members of the Humariaceae with well-developed hairs and later modified by Le Gal *(1947)* to include only those genera with red or yellow hymenia. Rooting or deeply embedded hairs are known in the Pezizales in only two other genera, *Scutellinia* and *Cheilymenia,* both members of the Ciliarieae *sensu* Le Gal. *Rhizoblepharia* was included in that tribe solely because of Rifai's contention that its hairs are of this type (the etymology of the generic name is self-explanatory).

During the Second Discomycete Exploration of the Neotropics in January, 1971, on the island of Jamaica, B.W.I., a Discomycete described here as a new species of *Rhizoblepharia* was collected. The new species, *R. neotropica,* differs from *R. jugispora* most obviously in that it is distinctly stipitate (FIG. 4). Though *R. jugispora* was originally described as "broadly sessile," my study of the type specimen has shown that it is at least distinctly substipitate (FIG. 3). The two species are similar in overall size, habitat, in the presence of stiff, pointed, thick-walled hairs (setae), in excipular structure, in non-blueing of the asci in Melzer's Reagent (J −), and in the essential features of the ascospores (differing notably in size between the two species), including the transverse wrinkling of the spore wall (FIG. 2). The arrangement of the hairs on the apothecium differs markedly between the two species.

A discussion of taxonomic criteria in the genus, and of generic relationships, precedes the formal taxonomic portion of this paper.

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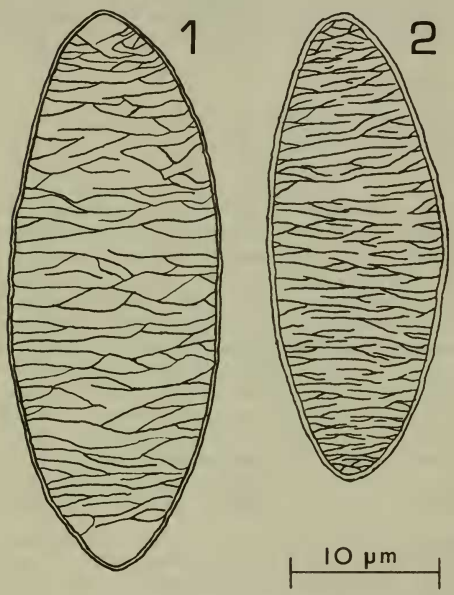
SOME TAXONOMIC CRITERIA IN RHIZOBLEPHARIA

HAIRS

ROOTING HAIRS:

A feature held in high regard taxonomically is the so-called rooting hair. These are a diagnostic feature of *Scutellinia*, but also occur in several species of *Cheilymenia*, a closely related genus. Rooting hairs are typically thick-walled, dark brown, septate, acuminate, and arise deep within the sterile tissues near the junction of the ectal and medullary excipula. Frequently the bases of the hairs are bifurcate, but division into 3, 4, 5 or more parts is not uncommon (Boudier, *1905-10:* pl. 368, 370, 371, 373-378, 384, 385; Denison, *1961*). The presence of hairs with furcate bases raises the interesting yet surprisingly little investigated question of how such development takes place.

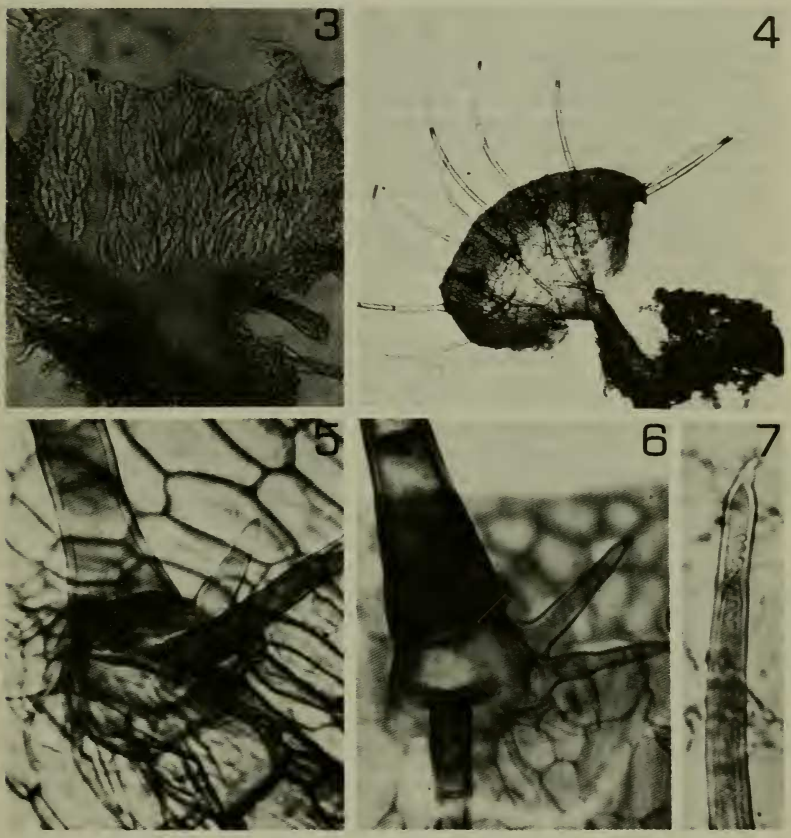


FIGS. 1-2. Camera lucida drawings of ascospores of *Rhizoblepharia* spp. × 2000. FIG. 1. *R. jugispora*. FIG. 2. *R. neotropica*.

Massee *(1897)* likened the development of rooting hairs in various species of *Scutellinia* (as *Lachnea*) to the process described by Dangeard *(1894)* for ascus formation in *Peziza vesiculosa* Bull. That is, the tips of two hyphae, "gametes," coalesce and their nuclei fuse to form an "oospore." This is followed by divisions of the fusion nucleus, and the subsequent movement of these nuclei into the gradually elongating hair (ascus). Massee held that more than two "gametes" could fuse, thus producing multiple divisions of the hair bases.

Gwynne-Vaughan and Williamson *(1933)* offered an explanation for rooting hair formation in *Scutellinia scutellata* (L. per St.-Amans) Lamb. comparing the process again to ascus formation, but rather to that in *Pyronema confluens* (Pers. per Pers.) Tul., in which crozier

formation takes place. Thus the hair would arise from the elongation of an intercalary cell of a recurved hypha with the adjacent cells giving the characteristic forked appearance of the base. In answer to the problem of how more than two basal branches could be formed from



FIGS. 3-7. Photomicrographs of *Rhizoblepharia* spp. FIG. 3. *R. jugispora,* from holotype material. Vertical section of apothecium, showing stipe, × 135. (Note displaced hair at lower right.) FIGS. 4-7. *R. neotropica,* from holotype material. FIG. 4. Vertical hand section of apothecium showing stipe and setae, × 45. FIGS. 5, 6. Piliferous cells; note widely diverging setae, × 350. FIG. 7. Internal proliferation of a hair, × 350.

such a mechanism, they offered the following explanation: "Additional branches may grow out, either as lateral supports or in search of further nutriment ...."

There is no evidence to support Massee's contention that in hairs the nuclei fuse in the formation of an "oospore," nor Gwynne-Vaughan and Williamson's theory that the hairs are intercalary on growing hyphae, since no free growing apices of such postulated hyphae have been reported. Professor E. J. H. Corner *(pers. comm.)*, however, thinks that the rooting hairs of *Scutellinia* are probably formed from the fusion of separate hyphal strands, and that the number of basal branches of a hair is indicative of the number of separate hyphal strands which fused during the early development of the hair. His unpublished note on this phenomenon was given to Mme Le Gal some years ago; she has indicated (Le Gal, *1953:* 117) that she intends to include this in her monographic treatment of the genus, soon to be published.

In *Rhizoblepharia jugispora* the hairs have been described by Rifai as rooting. They do arise, because of the reduced nature of the ectal excipulum, near the junction of the ectal and medullary excipula, but the bases of the hairs are not divided. They arise as single outgrowths from a superficial, usually swollen cell which is here termed a PILIFEROUS CELL. At the margin of the apothecium, the piliferous cells usually retain their turgidity, allowing the origin of the hairs to be easily demonstrated. Farther down the receptacle the piliferous cells either do not become swollen or do so and later collapse, making detection of the origin of these hairs much more difficult. The uppermost portion of the piliferous cell is pigmented and thick-walled where it gives rise to the hairs, giving the base of the hairs a distinctly flared appearance. Such bases might easily be misinterpreted as being furcate, especially when the thin-walled, hyaline, lower portion of the piliferous cell is collapsed. In *R. neotropica* the piliferous cell is usually much more swollen than in *R. jugispora,* allowing one to determine the origin much more easily. Such hairs may not correctly be called "rooting," because of their different ontogeny and consequent lack of a divided base. They may best be termed "superficial," because they arise from the outermost tissue layer. It should perhaps be noted that in *Rhizoblepharia,* because the ectal excipulum is so reduced that the hairs actually arise at the junction of the two excipula, such hairs might be more closely related to the rooting hairs of *Scutellinia* and *Cheilymenia* than to the superficial hairs of *Trichophaea* and *Humaria.*

STELLATE HAIRS:

Stellate hairs in the Pezizineae differ from rooting hairs in being borne superficially and in lacking a furcate base. They are composed of several (2-5) diverging branches which arise from a usually swollen basal cell. Stellate hairs may be interspersed among rooting hairs as in *Cheilymenia stercorea* (Pers. per Fr.) Boud. and *C. cruciplia* (Cke. & Phill. in Cke.) Le Gal, but are easily distinguished by their charac-

teristic stellate or cruciate appearance (Boudier, *1905-10:* pl. 384; Denison, *1964*).

In *Rhizoblepharia neotropica* a somewhat different type of stellate hair has been noted. The swollen, piliferous cell gives rise to one major seta, usually pointing upwards, and one to several, very reduced, widely diverging minor branches (FIGS. 5, 6).

Trichophaea bicuspis (Boud.) Boud. has yet another type of branched hair which might possibly be termed stellate, but which arises inconspicuously from a single superficial hyaline cell or a row of 2 or 3 cells (Kanouse, *1958*). The hairs are usually two-pronged, with the major branch diverging widely from and often forming in a direct line with the smaller branch or spur, thus giving the appearance of a single straight or slightly bent hair with two pointed ends. However, not infrequently, interspersed among the more numerous branched hairs are undivided ones. Such unbranched hairs could scarcely be called stellate, though they are doubtless a variation of the more frequent, two-pronged condition. Two, exceptional, three-pronged hairs were illustrated by Boudier (*1905-10:* pl. 366).

PROLIFERATING HAIRS:

Internal proliferation, or growth of a smaller, but apparently otherwise normal, seta enclosed completely within a larger seta has been described as occurring in various species of *Scutellinia* (Denison, *1961).* During the course of this study internal proliferation was observed in the setae of *Rhizoblepharia neotropica* (FIG. 7) and *Trichophaea bicuspis,* but was not observed in *R. jugispora.* The cause and function of internal proliferating hairs is not known, but Denison suggests that it might be "associated with damage of the larger enclosing hair."

ASCOSPORES

The uniqueness of the ascospore markings in *Rhizobelpharia* is easily attested to by the fact that it is the only genus in the suborder Pezizineae characterized by transversely wrinkled ascospores. One apparently undescribed species of *Pyronema* (Korf, *pers. comm.*), not at all closely related to *Rhizoblepharia,* also has transversely wrinkled ascospores. In both of the species of *Rhizoblepharia* the wrinkling, which is much more delicate in *R. neotropica* (FIG. 2) than in *R. jugispora* (FIG. 1), may even give the appearance of a poorly defined reticulum. In addition, the ascospores of both species are fusoidal, nonguttulate, hyaline to subhyaline, and the wrinkled inner wall and smooth outer wall are cyanophobic in Poirrier's Blue (cotton blue) dye. The ascospores of *R. jugispora* are slightly larger, and bear germpore-like marks near the ends of some ascospores as illustrated by Rifai. While the nuclear condition of the ascospores is unknown for *R. jugispora,* material of *R. neotropica* preserved in FAA in the field at the time of the original collection shows the uninucleate condition of the ascospores even in cotton blue or in Melzer's Reagent.

ECTAL EXCIPULUM

In attempting to use features of the excipulum in determining affinities, the characteristics of the ectal excipulum proved to be more important than those of the medullary excipulum. The ectal excipulum is reduced to a one-cell-thick layer or "skin" in *R. neotropica.* Though individual cells vary widely in shape in this species, from horizontally elongated at the margin to vertically elongated in the stipe, rows of cells in a more or less vertical orientation can always be distinguished. This corresponds very closely to the condition in *Trichophaea bicuspis* in which the ectal cells again form a one-cell-thick "skin," but are more uniform in size and shape, and are more tightly compacted into more strictly vertical rows. The term "skin" is used in describing the ectal excipulum of these two species because the tissue is only one cell thick and the cells tend to cohere in large, relatively intact fragments when making a crush mount of an apothecium. The ectal excipulum of *R. jugispora* approaches the extremely reduced condition of *R. neotropica* and *T. bicuspis,* but may be several cells thick and the cells seem to lack obvious vertical orientation. Because the material was scanty, only one apothecium of the type collection was sectioned, and the ectal excipulum was not observed clearly in face view. It may be more comparable to that of the other two species than appears in sectional view.

THE QUESTION OF CAROTENOIDS

Rifai's presumption that *Rhizoblepharia* has rooting hairs was undoubtedly the basis for his decision to place it near *Scutellinia* and *Cheilymenia* in the Ciliarieae. Up until then, however, all species described with rooting hairs had, in addition, yellowish to reddish carotenoid pigments in the hymenium. The carotenoids are generally concentrated in the paraphyses and tend to become faded or leached out entirely in dried specimens. Since present-day classification schemes for Operculate Discomycetes (Arpin, *1968;* Dennis, *1968;* Eckblad, *1968;* Korf, *1972*) continue to attach a high significance to the presence or absence of carotenoids in the hymenium, the question of whether or not a fungus might have had them in the fresh state is vital. Rifai opted for the presence of carotenoids in *Rhizoblepharia* although he had at his disposal only dried specimens which showed no evidence of their presence.

The discovery of a second species of the genus which totally lacks any hymenial pigments leads me to the opposite conclusion with regard to Rifai's type species, *R. jugispora.* I would therefore consider the genus *Rhizoblepharia* to lack carotenoids, and emend the generic diagnosis accordingly.

RELATIONSHIP TO TRICHOPHAEA BICUSPIS

In the course of examining several genera for possible close relationships to *Rhizoblepharia,* I examined the genus *Trichophaea* rather

closely. One species, *T. bicuspis*, long considered by Korf to be an anomalous member of that genus, showed characteristics in common with *Rhizoblepharia*, and with *R. neotropica* in particular. The species seems more closely related to *Rhizoblepharia* than to any species of *Trichophaea*, and in another paper (Korf and Erb, *1972*) a new genus, *Trichophaeopsis*, is being proposed to accommodate *Trichophaea bicuspis*.

RELATIONSHIP TO THE TRIBE PSEUDOMBROPHILEAE

At one time almost all hairy Operculate Discomycetes were placed in the genus *Lachnea (= Patella)*. The genus has since been divided, with species being distributed among genera such as *Scutellinia*, *Cheilymenia*, *Trichophaea*, *Humaria*, *Tricharina*, etc. *Rhizoblepharia* must be transferred from the Scutellinieae (= Ciliarieae) because of its lack of carotenoid pigments. The possibility of placing the genus near *Humaria* and *Trichophaea* in the Mycolachneeae is also rejected on the basis that the ascospores lack oil guttules. Instead it is proposed to transfer *Rhizoblepharia* to the tribe Pseudombrophileae as erected by Korf *(1972)*, within the family Pyronemataceae, subfamily Ascophanoideae. This tribe contains genera which lack carotenoid pigments and have shallow-cupulate to discoid apothecia beset with brown hyphae or brown setae, and ascospores devoid of oil guttules. The genus seems most closely related to *Trichophaeopsis*, and possibly to *Tricharina*.

TAXONOMY OF RHIZOBLEPHARIA

EMENDATION OF THE GENUS

R H I Z O B L E P H A R I A Rifai emend. Erb

= *Rhizoblepharia* Rifai *in* Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect., *57(3)*: 104. 1968.

TYPE SPECIES: *R. jugispora* Rifai, *Ibid.*, 105. 1968. (monotype)

Apothecia gregarious, minute, stipitate to substipitate. Disc shallowly concave or flat. Receptacle saucer-shaped, beset with numerous dark brown, septate, acuminate, thick-walled setae, at the margin arising directly upon a swollen, globose piliferous cell, elsewhere piliferous cells enlarged or not, often becoming collapsed and indistinct. Hyaline superficial hairs sometimes also present. Ectal excipulum of large, isodiametric or elongated, polygonal, subglobose or rectangular cells, of textura angularis primarily, becoming more vertically elongated and tending toward textura prismatica in the stipe. Medullary excipulum scant to well-differentiated, of compact, coarse, short-celled, constricted hyphae forming a textura intricata. Asci cylindrical, 8-spored, unitunicate, apex not blued in Melzer's Reagent, operculate, narrowed basally to a crozier or not. Ascospores uniseriate or biseriate, fusoidal to elliptic-fusoid, non-guttulate, hyaline to pale yellow, ornamented with delicate transverse and sometimes anastomosing cyanophobic wrinkles or ridges on the inner wall which may

form a germpore-like mark at the ends of the ascospores, the outer wall smooth and cyanophobic. Paraphyses slender, septate, apex not or slightly enlarged, straight, branched apically or not. Habitat: soil.

DIAGNOSIS OF THE NEW SPECIES

Rhizoblepharia neotropica Erb & Korf, sp. nov.

Apothecia minuta, stipitata, gregaria vel caespitosa. Discus pallidus vel albidus, planus vel concavus, 0.6-0.9 mm diam. Stipes cylindricus, 0.4 mm longus × 0.08 mm diam. Receptaculum et stipes concolores, pallidi vel albidi cum desiccati sunt, setis crassitunicatis, fuscis, usque ad 650 µm longis × 6-18 µm diam. induti, his setis vel singulatim vel in fasciculis setae unius majoris cum setis singulis pluribusve divergentibus minoribus ex cellulis globosis subglobosisve piliferis 20-55 µm diam. orientibus. Excipulum ectale cellulam unam crassitudine aequans, ex textura angulari formatum, cellulis 2-30 × 6-25 µm, stipite ex textura prismatica formato, cellulis 12-60 × 5-25 µm. Excipulum medullare exiguum, ex textura intricata formatum, hyphis 2-5 µm diam. Hymenium usque ad 165 µm crassum. Asci octospori, clavati, 125-175 × 15-20 µm, ad basin in crocam angustati, ad apicem operculati, (J —). Ascosporae hyalinae, uninucleatae, 30-35 × 9-11 µm, biseriatae, elliptico-fusoideae, eguttulatae, pariete exteriore laevi, cyanophobico, interiore transversaliter corrugato, cyanophobico. Paraphyses septatae, ramosae, apicibus 1-1.5 µm diam.

Habitat in solo, Jamaica, B. W. I.

Apothecia minute, short-stipitate, gregarious to caespitose (FIG. 4). Disc flat to somewhat concave (inrolled at the margin when dried), 0.6-0.9 mm in diam. Stipe distinct, cylindrical, up to 0.4 mm long and 0.08 mm in diam. Stipe, receptacle and disc concolorous, pallid to white when dried, more or less colorless and translucent when fresh. Receptacle and stipe beset with stiff, dark brown, thick-walled setae 150-650 × 6-18 µm in diam, which form a fringe at and extend beyond the margin. Hairs arising from piliferous cells of the ectal excipulum, acuminate, with up to 15 dark brown, thick-walled, transverse septa, some hairs (broken?) proliferating internally, especially near the apex (FIG. 7). Piliferous cells globose to subglobose, 20-55 µm in diam, bearing one major hair, and often one to several widely diverging hairs, hyaline below, becoming dark brown and thick-walled at and between the bases of hairs (FIGS. 5, 6).

Ectal excipulum of a single layer of cells forming a "skin" of textura angularis, arranged in loosely organized vertical rows. Marginal cells horizontally elongated, 2-20 × 6-25 µm, those farther down on the flanks becoming isodiametric to more vertically elongated, 12-30 × 6-18 µm, cells at the base of the receptacle and composing the stipe vertically elongated, 12-60 × 5-25 µm, tending toward textura prismatica. Medullary excipulum scant, of textura intricata, cells 2-5 µm in diam, not distinguishable from the subhymenium; hymenium up to 165 µm thick.

Asci 8-spored, clavate, 125-175 × 15-20 µm, narrowed basally to a crozier, the terminal cell usually not re-fusing with the antepenulti-

mate cell, apex not blueing in Melzer's Reagent (J —). Ascospores biseriate, elliptic-fusoid, nonguttulate, hyaline, uninucleate, 30-35 × 9-11 µm, with a double wall; the outer wall smooth and cyanophobic, the inner wall delicately transversely wrinkled at maturity and cyanophobic (FIG. 2).

Paraphyses branched, sparingly near the base, becoming very branched and entangled apically, septate, apices rounded but not enlarged, 1-1.5 µm in diam.

Habitat and Distribution: on soil, Jamaica, B. W. I.

HOLOTYPE: CUP-MJ *174*. On soil, along Lady's Mile Trail south of Woodcutter's Gap, vicinity of Newcastle, border of St. Andrew and Portland parishes. 9. I. 1971. *R. P. Korf, J. R. Dixon, K. P. Dumont, R. W. Erb, D. H. Pfister, D. R. Reynolds, A. Y. Rossman, & G. L. Samuels.*

PARATYPE: CUP-MJ *255*. On soil, vicinity of Dick's Pond, west of Hardwar Gap, near Holywell Recreation Area and Wag Water River, St. Andrew Parish, elev. 2800-3000 ft. 10. I. 1971. *R. P. Korf, et al.*

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SUMMARY

A new species, *Rhizoblepharia neotropica* Erb & Korf, is described from Jamaica, B.W.I. It has setae arising usually in widely diverging groups from a swollen piliferous cell (new term) on a distinctly stipitate apothecium. A reinvestigation of the type species of the genus, *R. jugispora* Rifai, demonstrated that in that species, too, the setae arise from piliferous cells, and are not "rooting" as originally described; the apothecia are substipitate rather than "broadly sessile" as given in the original diagnosis. No hymenial pigments occur in the neotropical species, and though carotenoid pigments were presumed to be present in the type species by Rifai, the genus is now emended to indicate that such pigments are lacking, as well as to incorporate the characters of the neotropical species and to correct observations on the type species. The genus is now to be assigned to the tribe Pseudombrophileae (Pyronemataceae, Ascophanoideae).

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